LANTERNFISHES OF THE SOUTHERN BENGUELA REGION

PART 1

FAUNAL COMPLEXITY AND DISTRIBUTION

By

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(With 2 figures and 8 tables)

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ABSTRACT

Various sampling cruises in the southern Benguela region (28°40′S–40°00′S 10°00′E–20°00′E) yielded a total of more than 17 000 lanternfishes (family Myctophidae). These comprise 65 species in 23 genera. Their horizontal distribution in the region is discussed in terms of their known Atlantic and Indo-Pacific ranges and their vertical distribution in relation to oceanic and pseudoceanic zonality. Results indicate that inshore of the 300 m isobath, lanternfishes are represented by a single, pseudoceanic species, *Lampanyctodes hectoris*. Oceanic species occur where bottom depths exceed this value. The sampling strategies employed preclude investigation of the diurnal relationship between mesopelagic and bathypelagic species. The southern Benguela region can be characterized as a transition zone rather than a subtropical zone. There is a strong intrusion of convergence and semisubantarctic species in association with cold-core eddies from the south, and a much weaker advection of tropical and broadly tropical species in Agulhas Water. A first estimate of the offshore lanternfish stock for the eastern South Atlantic is calculated as $8–12 \times 10^6$ tonnes which represents 50–70 per cent of the total estimated mesopelagic fish stock of the offshore eastern South Atlantic.

CONTENTS

INTRODUCTION

In order to assess the status of commercially exploited marine resources, the Sea Fisheries Research Institute (SFRI), Cape Town, has an ongoing series of routine sampling cruises in the eastern South Atlantic. Material and data arising from these cruises play a significant role in the CSIR–SANCOR-sponsored Benguela Ecology Programme, in which the structure and dynamics of the

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Benguela Upwelling System is being investigated. Lanternfishes (family Myctophidae) are a regular and abundant component of the catch from both the pelagic and benthic sampling. They represent not only an important group of trophic organisms within the system, but also represent an alternative fishery resource to more conventional species like anchovy *(Engraulis capensis)* and pilchard *(Sardinops ocellata)*.

Ahlstrom *et al.* (1976) reported that in the eastern Atlantic myctophids comprise nearly 10 per cent of all fish larvae caught between 19° and 26°S, with larval abundance values greater than 10 larvae/m^2 for the period August 1973 to April 1974. Recent surveys have indicated a larger proportion of myctophid larvae (29%) in Bongo net catches off the west coast (R. A. Cruickshank pers. comm.). Lanternfishes (mainly *Lampanyctodes hectoris*) were first recorded in the South African purse-seine catches in 1969, when 1 134 tons were taken (0,3% of the total catch). Subsequently, the catch has fluctuated, with a maximum of 42 560 tons being taken in 1973 (10,45%) (De Villiers 1982). A fishing quota of 50 000 tonnes has been allocated for the 1985 season.

Hulley (in press) has pointed out that there are 28 genera and 125 species of myctophid known, or likely to be found, in the southern African region, and has given a general account of their taxonomy and distribution. Some results have also been presented on the myctophid fauna of the southern Benguela region (Hulley 1972*a*, 1972*b*, 1981, 1986), but data from recent cruises allow for a more critical investigation of the structure and distribution of the lanternfish fauna. Rubiés (1985) has recently examined the myctophid fauna off the South West African–Namibian coast, recording a total of 41 species. Twenty-five of these species were taken only from the Valdivia Bank area on the Walvis Ridge, ten species only from the Benguela area, and six species were common to both areas.

The purpose of this paper is threefold: firstly, to establish the myctophid species complexity in the southern Benguela region, i.e. between 28°40′S (mouth of the Orange River) and 40°00′S, and between 10°00′E and 20°00′E; secondly, to examine the nature of the distribution patterns of these species, including both the oceanic and pseudoceanic zones; and thirdly, to obtain a first estimate of lanternfish abundance in the offshore area (greater than 100 miles offshore) of the South-east Atlantic. Here the total offshore mesopelagic fish stock has been estimated at 16×10^6 tonnes (Gjøsaeter & Kawaguchi 1980).

Investigations of the biology of *Lampanyctodes hectoris*, leading to estimates of inshore lanternfish abundance for the same region, are to be made independently by scientists at the Sea Fisheries Research Institute, Cape Town; these will be reported separately.

The areal choice in the present paper should also allow for the examination of distributional phenomena across the frontal zone(s) between upwelled Benguela Water and South Atlantic Central Water in the region of the shelf break at 300–500 m (Shannon 1985), but this aspect will be more fully developed in later publications.

MATERIAL AND METHODS

Specimens and data on specimens from the following cruises and from stations occupied with the following gear within the region have been incorporated into the analysis:

Walther Herwig 1971—Transect II	(WH–71)	MT–1600	(March)
Walther Herwig 1971—Transect II		David Net	(March)
SFRI Hake Survey 1984	(HJUL84)	BT–180	(July)
SFRI Hake Survey 1985	(HJAN85)	BT–180	(January)
SFRI Phyllosoma Survey 1982	(PAUG82)	RMT–2	(August)
SFRI Phyllosoma Survey 1983	(PAUG83)	RMT–8	(August)
SFRI Phyllosoma Survey 1984	(PAUG84)	RMT–8	(August)
SFRI Anchovy Acoustic Survey 1983	(ANAC83)	RMT–8	(May)

In addition, the lanternfish material in the collections of the South African Museum, Cape Town, taken within the defined southern Benguela region, has been re-examined for the purposes of this paper. These specimens were taken with a variety of gear-types: neuston net; N100B; N200B; IKMT.

Gear-type abbreviations are as follows:

BT–180: German bottom trawl with 180′ headline and stocking
David net: modified David neuston sampler
IKMT: 10′ Isaacs-Kidd midwater trawl
MT–1600: Engel midwater trawl with 1 600-mesh circumference
RMT–2: rectangular midwater trawl with 2 m^2 mouth opening
RMT–8: rectangular midwater trawl with 8 m^2 mouth opening

All specimens were identified to species. Standard lengths (SL), and in certain instances preserved wet weights, were taken for each specimen, resulting in data on more than 17 000 specimens. Taxonomic details for individual species are not given. However, the *Smith's sea fishes* (SFSA) species number (Hulley in press) is given, so that readers may refer to that publication for those details.

For all cruises, daytime hauls were distinguished from night hauls on the basis of commencing after 06h00 or before 18h00 (local time). Myctophids were absent from six (86%) of the day hauls from PAUG82 and eight (57%) day hauls from PAUG83; no day hauls were undertaken during PAUG84. For the purposes of stock estimation, distribution pattern and subpattern catch rates (specimens/hour) were calculated for night hauls only, according to the method of Hulley & Krefft (1985), for species from each of the RMT–2 (PAUG82) and RMT–8 (PAUG83 and PAUG84) nets, and for both day (1 haul, fishing depth >1 000 m) and night hauls for species from the MT–1600 (WH–71) net. These catch rates were converted into abundances in specimens/1 000 m^3, assuming that each gear was 100 per cent effective for the duration of the haul, that the fishes were evenly distributed in the upper 1 000 m, and that the mouth areas and mean trawling speeds were 2 m^2 and 2,5 knots (RMT–2), 8 m^2 and 2,5 knots (RMT–8), and 300 m^2 and 3,5 knots (MT–1600). On the basis of SL/weight scatter plots for *Lampanyctodes hectoris* (Fig. 1) and inspection of the standard lengths of specimens taken by each gear, the mean weight of a fish from the RMT–2 samples was accorded a value of 0,2 g, from the RMT–8 samples a value of 0,5 g, and from the MT–1600 samples a value of 1,0 g. The area of the offshore South-east Atlantic region is taken as 160×10^{11} m^2 (Gjøsaeter & Kawaguchi 1980).

RESULTS

Haul data, which includes discrimination by depth and/or time of day, is given in Tables 1 to 6. Positive hauls indicate the presence of myctophids. Table 7 is a species list of Myctophidae for the southern Benguela region and incorporates the Atlantic distribution pattern and subpattern placement of each species according to Hulley (1981), the number of specimens examined for each species, and the SFSA species number.

BT–180

Catch data for this gear (Tables 1, 2) indicate that although sampling was carried out from depths less than 101 m to greater than 500 m, the major fishing effort was concentrated between depths of 101–200 m (35% of total) and 210–300 m (30–35%). During both cruises, stations were occupied mainly during daylight hours (95% of total number). Therefore, although the results for night hauls should be regarded as tentative, it would appear that the epibenthic (pseudoceanic) lanternfish fauna exhibits diurnal migration into the water column during this period, since no specimens were taken during the night at depths of maximum daytime abundance (101–300 m). Furthermore during the day myctophids were taken only in 41–52 per cent of the hauls, pointing to the possibility of an extremely patchy distribution (see below). The major component of the lanternfish catch throughout the year was *Lampanyctodes hectoris*, whose highest mean catch rates were in the 101–200 m and 210–300 m depth ranges. Day mean catch rates at these depths were 4,9 and 5,6 specimens/hour respectively in winter, and >153,9 and 73,6 specimens/hour respectively in summer, suggesting a marked seasonal variation in availability and/or distribution. More recent unpublished data from the winter (July) 1985 Hake Survey support this suggestion. In the 301–400 m, 401–500 m and >500 m depth strata, mean catch rates for *Lampanyctodes hectoris* were considerably lower (winter: 7,7; 1,1; 0,3 specimens/hour; summer: >13,8; >2,9; 0,0 specimens/hour respectively). Other myctophid species were taken in those bottom hauls fished at depths greater than 301 m (*Diaphus hudsoni* (2 specimens), *D. meadi* (1), *D. ostenfeldi* (1), *Electrona risso* (2), *Gymnoscopelus (Nasolychnus) piabilis* (2), *Scopelopsis multipunctatus* (1), *Symbolophorus barnardi* (4), *S. boops* (7)) but these probably represent contaminants as the net is heaved from depth, since mean catch rates for the individual species range only between 0,1 and 1,0 specimens/hour ($\bar{x} = 0,3$ specimens/hour) and there is a decrease in the percentage of negative hauls at depths below 301 m. The high percentage of

TABLE 1

Analysis of myctophid data from BT–180 net during SFRI Hake Surveys.
= number of hauls; + = number of positive hauls; − = number of negative hauls.

Cruise	Time (local)	Total			0–100 m			101–200 m			201–300 m			301–400 m			401–500 m			> 500 m		
		#	+	−	#	+	−	#	+	−	#	+	−	#	+	−	#	+	−	#	+	−
HJUL84	0600–1800	86	25	61	4	0	4	31	9	22	29	5	24	10	4	6	9	4	5	3	3	0
	1800–0600	2	0	2	0	0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0	0
HJAN85	0600–1800	100	34	66	10	0	10	34	9	25	29	10	19	13	5	8	12	9	3	2	1	1
	1800–0600	7	0	7	0	0	0	3	0	3	3	0	3	0	0	0	1	0	1	0	0	0

TABLE 2

Analysis of myctophid data from BT–180 net during SFRI Hake Surveys.
= number of hauls; SP = number of species; SPP = number of specimens.

Cruise	Total			Time (local)	0–100 m			101–200 m			201–300 m			301–400 m			401–500 m			> 500 m		
	#	SP	SPP		#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP
HJUL84	88	6	417	0600–1800	4	0	0	31	1	152	29	1	163	10	2	79	9	6	17	3	4	6
				1800–0600	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
HJAN85	107	6	>7585	0600–1800	10	0	0	34	1	>5234	29	1	>2135	13	4	>182	9	4	>33	2	1	1
				1800–0600	0	0	0	3	0	0	3	0	0	0	0	0	1	0	0	0	0	0

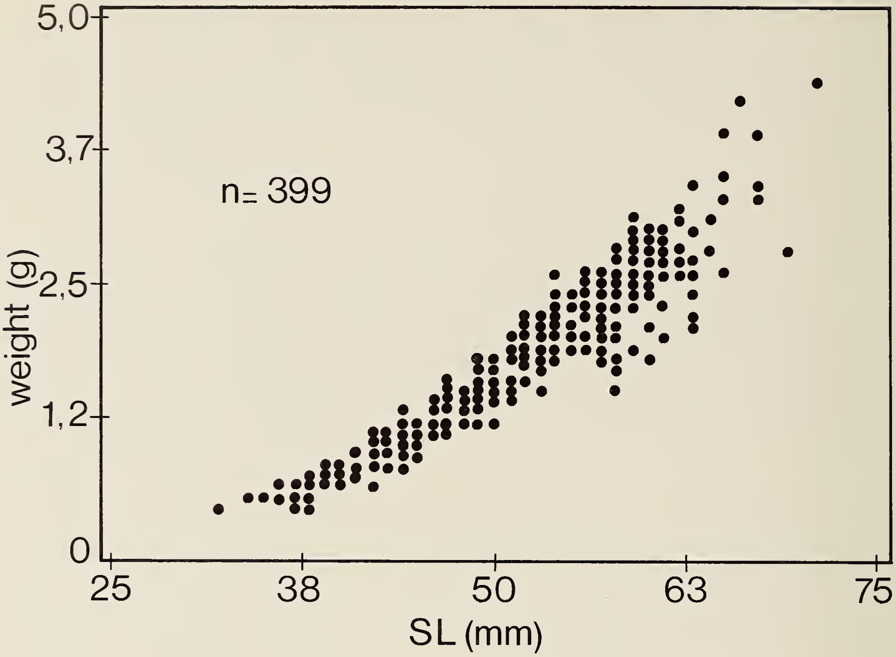

Fig. 1. Scatter plot of standard length (SL) versus preserved wet weight for *Lampanyctodes hectoris*.

negative hauls in the 101–200 m (71–73%) and 201–300 m (66–83%) depth strata can therefore only be accounted for by the absence of a single species, *Lampanyctodes hectoris*, and Index of Dispersion (ID) values (Wormuth & Roper 1983) considerably greater than 1,0 indicate that the distribution of *Lampanyctodes hectoris* is strongly patchy within its principal epibenthic distributional depth range (101–300 m). Further development of the data for this species is outside the scope of the paper, although it should be mentioned that *Lampanyctodes hectoris* was also taken in pelagic hauls, particularly those inside or immediately adjacent to the frontal system developed by the upwelled Benguela Water. These specimens are probably associated with the system of cold-core eddies generated at the front (Lutjeharms 1981*a*).

RMT–2 and RMT–8

Catch data for these nets from the SFRI Phyllosoma Surveys (PAUG82, PAUG83 and PAUG84) are given in Tables 3 and 4. The major sampling effort was directed at depths between 200–0 m and 75–0 m (63% of total) and only one haul was made below 500 m (day). RMT–2 nets also sampled the 10–0 m (11%) and 50–0 m (16%) strata—depths not specifically fished during the 1983 and 1984 RMT–8 sampling programme, although nine oblique hauls were made with the latter gear from a maximum depth of 250 m.

TABLE 3

Analysis of myctophid data from RMT–2 and RMT–8 nets during SFRI Phyllosoma Surveys.
A = number of hauls with opening–closing device fitted; B = number of oblique hauls to fishing depth;
SP = number of species; SPP = number of specimens.

Depth	RMT–2 1982						RMT–8 1983						RMT–8 1984						
(m)	A	SP	SPP	B	SP	SPP	A	SP	SPP	B	SP	SPP	A	SP	SPP	B	SP	SPP	*Group*
600–500	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	GROUP E 1 haul, 0 species 0 specimens
500–400	0	0	0	0	0	0	1	7	20	0	0	0	0	0	0	0	0	0	
500–0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	GROUP D
400–300	0	0	0	0	0	0	2	13	63	0	0	0	0	0	0	0	0	0	11 hauls
300–200	0	0	0	0	0	0	5	2	19	0	0	0	0	0	0	0	0	0	19 species
250–150	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	135 specimens
250–0	0	0	0	0	0	0	0	0	0	1	4	33	0	0	0	0	0	0	
200–100	0	0	0	0	0	0	3	12	46	0	0	0	0	0	0	0	0	0	
197	7	20	47	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
197–0	0	0	0	2	7	8	0	0	0	0	0	0	0	0	0	0	0	0	
150	8	20	64	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
150–10	0	0	0	0	0	0	1	3	6	0	0	0	0	0	0	0	0	0	
120–20	0	0	0	0	0	0	9	33	1 010	0	0	0	16	27	574	0	0	0	GROUP C
120–0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	19	196	77 hauls
100	9	25	197	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	48 species
100–25	0	0	0	0	0	0	2	16	165	0	0	0	0	0	0	0	0	0	2 881 specimens
100–10	0	0	0	0	0	0	1	14	72	0	0	0	0	0	0	0	0	0	
100–0	0	0	0	1	2	15	0	0	0	0	0	0	0	0	0	0	0	0	
80–0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
75	8	31	389	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
75–0	0	0	0	1	15	92	0	0	0	0	0	0	0	0	0	0	0	0	
50	8	29	533	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	GROUP B
50–0	0	0	0	2	11	106	0	0	0	0	0	0	0	0	0	0	0	0	19 hauls
25	8	20	395	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	30 species
25–0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1 034 specimens
10	4	7	62	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	GROUP A
10–0	0	0	0	2	2	10	0	0	0	0	0	0	0	0	0	0	0	0	14 hauls
1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11 species
0	0	0	0	7	5	14	0	0	0	0	0	0	0	0	0	0	0	0	86 specimens

TABLE 4

Analysis of myctophid data from RMT–2 and RMT–8 nets during SFRI Phyllosoma Surveys.
= number of hauls; + = number of positive hauls; – = number of negative hauls.

Gear		*Time (local)*	*Total*			*Group A*			*Group B*			*Group C*			*Group D*			*Group E*		
Year	#		#	+	–	#	+	–	#	+	–	#	+	–	#	+	–	#	+	–
RMT–2 1982	71	0600–1800	7	1	6	1	0	1	0	0	0	5	1	4	1	0	1	0	0	0
		1800–0600	64	57	7	13	8	5	19	18	1	32	31	1	0	0	0	0	0	0
RMT–8 1983	27	0600–1800	14	6	8	0	0	0	0	0	0	4	2	2	9	4	5	1	0	0
		1800–0600	13	12	1	0	0	0	0	0	0	12	11	1	1	1	0	0	0	0
RMT–8 1984	24	0600–1800	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
		1800–0600	24	23	1	0	0	0	0	0	0	24	23	1	0	0	0	0	0	0

RMT–2 data reveal a high proportion of negative daytime hauls (86% of PAUG82 cruise), the single positive sample (09h50: 150–0 m) yielding four specimens each of *Diaphus hudsoni* and *Lampanyctus lepidolychnus*. Negative daylight hauls with the RMT–8 were lower (57%) during the 1983 cruise (PAUG83); no daytime sampling was undertaken during PAUG84. Two positive daytime hauls (P 011: 06h31–07h31; P 024: 15h00–16h00) were made in the 200–0 m depth range during PAUG83 and yielded a total of 38 specimens *(Benthosema suborbitale, Ceratoscopelus warmingii, Diaphus hudsoni, D. meadi, Lampanyctus pusillus, Lobianchia dofleini, Metelectrona ventralis, Symbolophorus boops)*, while 102 specimens were recorded from the four positive daytime stations in the 500–0 m depth range during the same cruise. The species recorded at these latter stations were *Benthosema suborbitale, Ceratoscopelus warmingii, Diaphus effulgens, D. hudsoni, D. lucidus, D. meadi, D. metopoclampus, D. ostenfeldi, Diogenichthys atlanticus, Hygophum hygomii, Lampadena notialis, Lampanyctus alatus, L. pusillus, Lobianchia dofleini, Protomyctophum (Hierops) subparallelum, Scopelopsis multipunctatus* and *Symbolophorus barnardi*.

For night sampling, 89 per cent and 92–96 per cent of stations occupied with the RMT–2 and RMT–8 respectively, yielded lanternfishes. No definite scattering layer was observed at station 9 (4)—the single negative night station of the PAUG84 cruise, while the single negative night haul (P 003: 04h13–05h13) from the PAUG83 cruise was in 120–0 m. Seven negative night hauls were recorded during PAUG82, five (71%) of which were 10–0 m or at the surface; the net bar was bent during the single negative night haul (Station Number 002030) in the 50–0 m depth range. The number of hauls, number of species, and number of specimens for both gear during the PAUG82, PAUG83, and PAUG84 cruises is summarized in Table 3.

RMT–8 data from ANAC83 are included in Table 6. A total of 2 248 specimens was taken during this cruise, in which the net was aimed at target species, the duration of the haul being one hour, and the maximum fishing depth not exceeding 100 m. Thirty-eight specimens of *Lampanyctodes hectoris* from four hauls lack accurate depth data but have been included at the 0 m depth only for the sake of completeness. The four hauls in the 50–0 m fishing-depth range yielded 643 specimens of one species *(Lampanyctodes hectoris)*, but 35 hauls in the 100–0 m range caught 1 563 specimens of *Lampanyctodes hectoris*, two *Diaphus hudsoni*, and one specimen of each of *Diaphus meadi* and *Hygophum hanseni*. Further analysis of these data has revealed that species other than *Lampanyctodes hectoris* were caught in the upper 100 m only at those stations where the bottom soundings were in excess of about 500 m.

For *Lampanyctodes hectoris*, the highest mean catch rate (130,14 specimens/station; number of stations = 7) was obtained inside of the 100 m isobath. Between the 100 m and 200 m isobaths the mean catch rate was 52,76 specimens/station (n = 21); between 200 m and 300 m, 34,00 specimens/station (n = 3); between 300 m and 400 m, 15,25 specimens/station (n = 4);

between 400 m and 500 m, 11,33 specimens/station (n = 3); and greater than 500 m, 3,33 specimens/station (n = 3). These data suggest that, for RMT–8 hauls at least, the major pelagic concentrations of *Lampanyctodes hectoris* are shoreward of the 100 m isobath and that ID values are considerably greater than 1, i.e. a marked patchiness.

During this same cruise, two hauls were made at the surface with a neuston net and yielded a total of 147 *Symbolophorus boops*, five *Symbolophorus barnardi*, and one *Lampanyctodes hectoris*. Both hauls were deployed over bottom depths of 510–640 m.

MT–1600

During the course of Transect II of the 1971 cruise of FRV *Walther Herwig*, six stations were occupied in the defined area with an MT–1600 net (Table 5). Shallower hauls (112–0 m, 305–0 m, 592–0 m) were made at night, while a single deep haul (>1 000–0 m) was made during the day. A total of 2 310 specimens in 46 species was taken. Of these species, only *Diaphus richardsoni, Electrona carlsbergi, Lampanyctus lineatus* and *L. nobilis* were not collected by the other types of gear. *Lampanyctodes hectoris* was not recorded from any of the MT–1600 stations, which were situated at distances of greater than 95 sea miles offshore, where bottom depths exceeded 3 500 m. Hulley (1981) gave a breakdown of the species distributions at these stations.

Other gear

The myctophid specimens taken in the southern Benguela region during the deep-sea cruises of *Africana II* (Table 6: N200B, $IKMT_a$) have been described by Hulley (1972*a*). The nine IKMT oblique hauls (5 day; 2 night; 1 day–night (15h25–19h10); and 1 time unknown) from 1 000–0 m yielded 138 specimens comprising 29 species, while the single IKMT oblique haul (day) from 1 400–0 m yielded 16 specimens comprising nine species. The species *Lobianchia dofleini, Protomyctophum (Protomyctophum) andriashevi,* and *Scopelopsis multipunctatus*, taken in the latter haul, were not recorded from the shallower hauls. The single N200B haul (day) from 823–0 m yielded one specimen each of *Diogenichthys atlanticus* and *Lampanyctus alatus*, both species being recorded also from the IKMT samples of this cruise.

A haul analysis for the lanternfishes from the South African Museum's IK stations in the region (Grindley & Penrith 1965) is given in Table 6 ($IKMT_s$). The 26 stations (11 day; 15 night) occupied with the gear during the sampling programme yielded 141 specimens (18 species). Most stations (22) were positioned west of Slangkop (34°09′S 18°19′E). This material was reworked because of errors in identification and nomenclature (see synonymies in Hulley in press). No lanternfish specimens were obtained from the day hauls, fished obliquely to a maximum of 500 m. Myctophids were caught only at five of the night stations, the 82 specimens from the 0–50 m depth strata consisting of a single species, *Lampanyctodes hectoris*. The following species were taken in hauls

TABLE 5

Analysis of myctophid data from MT–1600 net from *Walther Herwig* stations in southern Benguela region.
= number of hauls; SP = number of species; SPP = number of specimens.

Gear		Total		Time		0–112 m			0–305 m			0–592 m			> 1 000 m		
Year	#	SP	SPP	(local)	#	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP
MT–1600 1971	6	46	2 310	0600–1800	1	0	0	0	0	0	0	0	0	0	1	17	196
				1800–0600	5	2	28	994	2	34	890	1	28	222	0	0	0

TABLE 6

Analysis of myctophid data from various nets deployed in the southern Benguela region.
= number of hauls; SP = number of species; SPP = number of specimens; * = no depth data.

Gear	Total			0 m			0–50 m			0–100 m			0–200 m			0–500 m			0–1 000 m			0–> 1 000 m		
	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP	#	SP	SPP
RMT–8 ANAC83	43	5	2 248	4*	1*	38*	4	1	643	35	4	1 567	0	0	0	0	0	0	0	0	0	0	0	0
Neuston	2	3	153	2	3	153	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
N200B	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	2	2	0	0	0
$IKMT_a$	10	32	154	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	29	138	1	9	16
$IKMT_s$	26	18	141	0	0	0	9	1	82	4	0	0	3	13	53	10	5	6	0	0	0	0	0	0
Other	11	6	355	8*	6*	346*	0	0	0	0	0	0	2	1	6	1	1	3	0	0	0	0	0	0
David	7	4	50	7	4	50	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

0–200 m and 0–500 m: *Diaphus brachycephalus, D. hudsoni, D. lucidus, D. meadi, D. metopoclampus, D. mollis, D. ostenfeldi, Hygophum hanseni, H. hygomii, Lampanyctus alatus, L. australis, L. lepidolychnus, Lobianchia dofleini, Protomyctophum (Protomyctophum) normani, Scopelopsis multipunctatus, Symbolophorus barnardi* and *Triphoturus nigrescens*.

Additional lanternfish material in the SAM collections (Table 6: Other) was obtained from 11 hauls occupied with a variety of gear including bottom trawls and N100B nets. Depth data (and in some instances gear type) were not available for eight of these hauls, but the 346 specimens taken by these hauls have been included in Table 6. These specimens comprise the following species: *Diaphus meadi* (1), *Gonichthys barnesi* (293), *Lampanyctodes hectoris* (3), *Lampanyctus lepidolychnus* (1), *Symbolophorus barnardi* (1), and *S. boops* (47). The single species recorded from the two N100B hauls (0–200 m) and the one BT haul (424 m) was *Lampanyctodes hectoris*. During the 1971 transect of FRV *Walther Herwig*, 50 lanternfish specimens were taken at the surface with a David net (Table 6): *Gonichthys barnesi* (42), *Myctophum asperum* (3), *M. nitidulum* (1) and *M. spinosum* (4).

DISCUSSION

Any discussion of distribution in the family Myctophidae should take into account that major ecological differences exist and that parameters affecting distribution patterns in one community may not necessarily be the same in another community. The community structure terminology used in this paper follows Hulley (1981), in which it is suggested that myctophids may be divided into (1) oceanic (= high-oceanic) mesopelagic and bathypelagic communities, and (2) pseudoceanic epibenthic and pelagic communities. However, the groupings within the pseudoceanic zone may not be as distinct. For example, it would appear from the above results that *Lampanyctodes hectoris*, which is at present regarded as a member of the pseudoceanic pelagic community, may be taken in abundance in bottom trawls during the day but may move off the bottom and into the upper 50 m of the water column during the night. A similar behaviour pattern has been reported for the Pacific pseudoceanic species *Diaphus watasei* in Suruga Bay (Kawaguchi & Shimizu 1978). Lanternfish community structure is further complicated by the fact that certain oceanic species, for example *Gymnoscopelus bolini, G. braueri, G. nicholsi, G. piabilis, Notoscopelus kroeyerii*, may be caught (? seasonally) on upper-slope and outer-shelf regions in potentially economic quantities (Dubrovskaya & Makorov 1969; Hulley & Krefft 1985). In addition, other oceanic species *(Diaphus dumerilii, Lampanyctus australis)* may possess pseudoceanic populations (Hulley 1981; Rubiés 1985). Comprehensive data on the life histories and reproductive biology of these species is sparse, and more research will be required before delineation of community structure in myctophids can be fully developed.

The interpretation of species complexity and general distribution in this paper is constrained both by a 'division of labour' aspect (i.e. SFRI is investigating the biology of *Lampanyctodes hectoris*) and by the variety of sampling strategies employed. Depths below 1 000 m were not well sampled (4 daylight hauls), and only 12 pelagic hauls (8 day; 3 night; 1 time unknown) and 6 bottom hauls (all during the day) were made to depths between 500 m and 1 000 m. Therefore, since bathypelagic species are poorly represented in the collections, the main thrust of the discussion will focus on the oceanic mesopelagic community.

The results of the present paper, particularly those from the BT–180 samples, confirm the distinction of at least a pseudoceanic lanternfish community and an oceanic community, the former characterized by *Lampanyctodes hectoris*. The data does not allow for closer inspection of the relationships between mesopelagic and bathypelagic species, except to indicate that there may be a degree of depth separation at night (see *Lampanyctus achirus* below). However, penetration of the upper 500 m of the water column by this bathypelagic species does take place in the southern Benguela region.

The physical structure of the seas around South Africa, in particular the South-east Atlantic and Benguela Upwelling Region, has been repeatedly described (see Shannon 1985) and does not need to be given here. Only features that are relevant to the interpretation of the distribution will be discussed.

Firstly, specimens of Indo-Pacific species are advected into the South-east Atlantic in water that originates from the Agulhas Current (Heydorn 1959; Krefft 1974; Weikert 1975; Hulley 1981, 1986; Bekker 1983; De Decker 1984). Thermal infra-red imagery has indicated that at least two mechanisms exist for this advection: (1) the growth, decay and dispersion of shearing eddies on the northern border of the Agulhas Current, with the subsequent advection of fragments into the South Atlantic; and (2) the production of Agulhas Water rings from the Agulhas Current retroflection area south-west of South Africa (Lutjeharms & Valentine 1981). On the basis of temperature recordings from a satellite-tracked buoy placed in an Agulhas Current fragment, these authors reported that the advected water lost its temperature characteristics (from 17 °C to 14 °C) over a period of 40 days, owing to mixing with colder South Atlantic water. Although Darbyshire (1966) has suggested that this advected Agulhas Water may be detected as far north as 23°S, its distinction from aged, upwelled Benguela Water at lower latitudes is difficult (Jones 1971). Shannon (1966) has indicated that the advection of this Agulhas Water is at a maximum during summer and autumn, and at a minimum during winter and spring.

Secondly, it would appear that some authors have characterized the offshore region of the eastern South Atlantic, north of the Subtropical Convergence, as subtropical (Boden 1951; Abrams *et al.* 1984; Abrams 1985). However, there is a substantial intrusion of convergence and subantarctic faunal elements into the southern Benguela region and even on to the South African shelf (Krefft 1974, 1978; Hulley 1981; McGinnis 1982; Bekker 1983; De Decker 1984), in association with the north-east deflection of the isotherms and isohalines (D.H.I. *Monatskarten* 1971). Drift-card observations have confirmed the northward flow of surface water from the Convergence towards the South African coast during the winter months (Shannon *et al.* 1973), while subsurface investigations have demonstrated the existence of a complex cold-core eddy system north of the Convergence to about 31°S (Visser 1969; Shannon & Van Rijswijck 1969; Welsh & Visser 1970; Henry 1975; Lenz 1975; Allanson *et al.* 1981; Lutjeharms & Emery 1983; Lutjeharms *et al.* 1985). These cold-core eddies, which are formed from planetary waves moving along the Convergence becoming unstable and losing their tops, drift northward (Lutjeharms 1981*b*). Although they extend to a depth well below 500 m and can be detected at 1 000 m, they become well mixed with South Atlantic water (Welsh & Visser 1970). This suggests the probability of mixed subtropical–temperate faunas in the study region and the possible existence of a transitional zone similar to that reported off Peru (Parin *et al.* 1973).

Bathypelagic species (Table 7)

Of the five bathypelagic species known from the Atlantic and Indian oceans *(Gymnoscopelus opisthopterus, Lampadena anomala, Taaningichthys paurolychnus, T. bathyphilus, Lampanyctus achirus)*, only the latter two species should occur in the southern Benguela region (Hulley 1981; Bekker 1983). Isolated specimens of the Antarctic species *Gymnoscopelus opisthopterus* have been taken in trawls fished to below 2 000 m as far north as 40°20′S (Hulley 1981), but sampling at these depths has not yet been undertaken in the southern Benguela region. The deepest haul included in the present survey (WH 417/71) was fished to 1 550 m. One specimen of *Taaningichthys bathyphilus* (58 mm SL) was recorded from 1 000–0 m at 30°19′S 10°08′E. *Lampanyctus achirus* was taken throughout the region (31°19′S–39°06′S and 10°08′E–17°11′E) and, except for a single case, in depths greater than 592 m. However, Hulley (1981) has pointed out that this species may be caught in depths shallower than 500 m in areas of pronounced upwelling, which may account for the record of the specimen (48 mm SL) at 33°44′S 17°11′E from 120 m.

Pseudoceanic species (Table 7)

These are species that are associated with land environments and land-orientated food chains and are distributed on or over continental shelf and slope regions and in the neighbourhood of oceanic islands. On a global basis, the following pseudoceanic species of Myctophidae have been recognized: *Diaphus adenomus, D. coeruleus, D. garmani, D. knappi, D. minax, D. roei, D. sagamiensis, D. suborbitalis, D. taaningi, D. umbroculus. D. watasei, Idiolychnus urolampus, Lampadena pontifex, Lampanyctodes hectoris,* and possibly *Diaphus burtoni* and *Myctophum fissunovi* (Krefft 1970; Nafpaktitis & Paxton 1968; Kawaguchi & Shimizu 1978; Nafpaktitis 1978; Hulley 1981; Bekker 1983; Rubiés 1985). Two of these species, *Diaphus garmani* and *Lampanyctodes hectoris*, have been taken in the southern Benguela region. The former species possesses a West tropical Subpattern in the Atlantic (Nafpaktitis *et al.* 1977; Hulley 1981) and in the Indian Ocean has been recorded from the coast of East Africa, the Comoro Islands, the west coast of Madagascar, off Mozambique, and to about 26°S (Nafpaktitis 1978; Gjøsaeter & Beck 1981; Hulley 1984). The single specimen taken during the present surveys, at 33°34′S 17°32′E (bottom depth 404 m), represents the first record of *Diaphus garmani* in the eastern South Atlantic. Its presence here appears to be associated with the advection of Agulhas Water into the region rather than an association with the bottom depth. An additional record at 36°33′S 20°01′E serves to link the distribution to that in the Agulhas Current. *Diaphus taaningi* is known from the Mauritanian Upwelling Region, Gulf of Guinea, and south to about 24°S (O'Toole 1976; Hulley 1981; Rubiés 1985; SAM data), while *Lampadena pontifex* has been caught at 24°26′S 13°30′E (Karrer 1975), between 23°30′S 12°45′E and 25°30′S 12°27′E (SAM data), and 'sporadically' to about 28°30′S (Rubiés 1985). These records suggest that the two species might be expected within the southern Benguela region as defined here.

Oceanic species (Table 7)

In addition to the four bathypelagic and pseudoceanic species, 61 oceanic mesopelagic species of Myctophidae were taken during the sampling in the southern Benguela region. These are listed in Table 7, which is based on the Atlantic Ocean distribution patterns and subpatterns given by Hulley (1981).

Bekker (1983) recorded the following species from the region, but no specimens of these were taken during the sampling cruises of the present survey: *Bolinichthys photothorax, Diaphus holti, D. termophilus, D. problematicus, Electrona antarctica, Gonichthys venetus, Gymnoscopelus fraseri, G. braueri, Lampadena dea, L. chavesi, L. urophaos, Myctophum obtusirostre, Taaningichthys miminus*. However, recent investigations indicate that *Diaphus holti, Lampadena dea* and *L. chavesi* are known from off the South West African–Namibian coast (Rubiés 1985).

Species that have a Broadly Tropical distribution pattern in the Indian Ocean *(Diaphus parri, D. richardsoni, Diogenichthys panurgus, Lampanyctus turneri, Myctophum spinosum, Triphoturus nigrescens)* manifest themselves in the Agulhas Subpattern of the Atlantic Ocean. These species, together with *Diaphus diadematus* (Extended Agulhas Subpattern), are advected in Agulhas Water pockets into the southern Benguela region and also, in the case of the latter species, may be associated with aged upwelled Benguela Water. None of these species was recorded by Rubiés (1985) off the South West African–Namibian coast. In a similar manner, Atlantic holotropical species *(Bolinichthys supralateralis, Diaphus luetkeni, Lampanyctus nobilis)*—which are more widely distributed in the Indo-West Pacific—thermophilic-eurytropical species *(Diaphus brachycephalus, D. lucidus, D. perspicillatus, D. splendidus, Myctophum nitidulum)*, and possibly certain holoeurytropical species *(Myctophum selenops)*, penetrate the southern Benguela region with Agulhas Water.

TABLE 7

Analysis of myctophid data from all types of gear. Distributional patterns and subpatterns after Hulley (1981).

Pattern	Subpattern	Species	No. specimens	SFSA No.
OCEANIC BATHYPELAGIC				
Widespread		*Taaningichthys bathyphilus*	1	86.123
Temperate	South Temperate Subantarctic	*Lampanyctus achirus*	45	86.73
PSEUDOCEANIC PELAGIC				
Tropical	West Tropical	*Diaphus garmani*	1	86.19
Benguela		*Lampanyctodes hectoris*	>10 842	86.72
OCEANIC MESOPELAGIC				
Widespread		*Diogenichthys atlanticus*	144	86.42
		Electrona risso	18	86.47
		Lobianchia dofleini	391	86.92
		Notolychnus valdiviae	69	86.106
Broadly Tropical	Holoeurytropical	*Ceratoscopelus warmingii*	366	86.9
		Diaphus mollis	46	86.28
		Lampanyctus photonotus	3	86.83
		Lobianchia gemellarii	33	86.93
		Myctophum selenops	4	86.104
		Notoscopelus resplendens	124	86.108
	Thermophilic-eurytropical	*Diaphus brachycephalus*	7	86.13
		Diaphus lucidus	71	86.23
		Diaphus perspicillatus	11	86.32
		Diaphus splendidus	2	86.37
		Myctophum nitidulum	2	86.101
	Thermophobic-eurytropical	*Benthosema suborbitale*	102	86.3
		Lampanyctus alatus	155	86.74
		Lampanyctus lineatus	1	86.80
	Agulhas	*Diaphus parri*	3	86.31
		Diaphus richardsoni	2	86.35
		Diogenichthys panurgus	1	86.43
		Lampanyctus turneri	13	86.87
		Myctophum spinosum	4	86.105
		Triphoturus nigrescens	6	86.125
	Extended Agulhas	*Diaphus diadematus*	96	86.14
Tropical	Holotropical	*Bolinichthys supralateralis*	5	86.7
		Diaphus luetkeni	3	86.24
		Lampanyctus nobilis	2	86.82
		Myctophum asperum	3	86.98

OCEANIC MESOPELAGIC *(contd)*

Subtropical	Bisubtropical	*Bolinichthys indicus*	20	86.4
		Diaphus effulgens	14	86.16
		Diaphus metopoclampus	46	86.27
		Hygophum hygomii	179	86.61
		Lampanyctus ater	55	86.75
		Lampanyctus festivus	33	86.77
		Lampanyctus pusillus	306	86.84
	South subtropical	*Myctophum phengodes*	23	86.103
		Scopelopsis multipunctatus	172	86.118
		Symbolophorus barnardi	162	86.119
Temperate	Bitemperate	*Lampadena speculigera*	12	86.71
		Lampanyctus intricarius	9	86.78
		Lampanyctus macdonaldi	1	86.81
		Loweina interrupta	1	86.94
	South temperate Convergence	*Diaphus meadi*	1 436	86.26
		Diaphus ostenfeldi	15	86.30
		Gonichthys barnesi	335	86.49
		Hygophum hanseni	22	86.60
		Lampadena notialis	22	86.69
		Lampanyctus australis	420	86.76
		Lampanyctus lepidolychnus	278	86.79
		Lampanyctus sp. B	9	86.89
		Lampichthys procerus	287	86.90
		Protomyctophum normani	4	86.116
		Protomyctophum subparallelum	11	86.110
	Subantarctic holosubantarctic	*Electrona carlsbergi*	2	86.45
		Protomyctophum andriashevi	1	86.111
		Protomyctophum parallelum	1	86.109
	Subantarctic semisubantarctic	*Diaphus hudsoni*	472	86.20
		Gymnoscopelus piabilis	8	86.58
		Metelectrona ventralis	45	86.96
		Symbolophorus boops	316	86.120

Table 8 gives catch rates for each of the pattern types on the basis of four cruises, during which RMT–2 (PAUG82), RMT–8 (PAUG83, PAUG84), and MT–1600 (WH–71) nets were deployed. The percentage contribution for each of the patterns and subpatterns, based on the mean catch rate (specimens per 1 000 m^3) is given in Figure 2.

Catch rates for the Thermophilic-eurytropical, Agulhas, Extended Agulhas and Holotropical subpatterns are low (Table 8), suggesting that all of the above species show a 'tailing' distribution (i.e. a decline in density with increasing latitude—see Hulley 1981, figs 39, 56, 67, 95) in the Agulhas Current, with a correlated low abundance value in the eastern South Atlantic. It should be noted that specimens of *Myctophum asperum, M. nitidulum* and *M. spinosum* were taken at the surface during sampling with a David net. The seasonality of occurrence of such species in this region will be examined in a later paper.

TABLE 8

Catch rates, percentage contribution and stock estimate for oceanic mesopelagic species of Myctophidae from SFRI Phyllosoma Surveys and from *Walther Herwig* stations in the southern Benguela region. Patterns and subpatterns after Hulley (1981).

Pattern	*Subpattern*	*Catch rate* (specimens/1 000 m³) PAUG82 RMT–2	PAUG83/84 RMT–8	WH–71 MT–1600	*Mean*	%
Widespread		0,3188	0,0372	0,1192	0,1586	9,67
Broadly Tropical	Holoeurytropical	0,1889	0,2079	0,0599	0,1522	9,28
	Thermophilic-eurytropical	0,0202	0,0124	0,0216	0,0181	1,10
	Thermophobic-eurytropical	0,2986	0,0365	0,0035	0,1129	6,88
	Agulhas	0,0101	0,0022	0,0041	0,0055	0,34
	Extended Agulhas	0,0186	0,0080	0,0261	0,0176	1,07
Tropical	Holotropical	0,0034	0,0022	0,0009	0,0022	0,13
Subtropical	Bisubtropical	0,3876	0,0496	0,0968	0,1780	10,85
	South subtropical	0,3475	0,0285	0,0285	0,1348	8,22
Temperate	Bitemperate	0,0219	0,0015	0,0017	0,0084	0,51
	South Temperate (Convergence)	0,9144	0,4676	0,3548	0,5789	35,29
	Subantarctic (Holosubantarctic)	0,0000	0,0000	0,0007	0,0002	0,01
	Subantarctic (Semisubantarctic)	0,6866	0,1160	0,0163	0,2730	16,64
Gear catch rate		3,2166	0,9696	0,7341		
Mean specimen weight (g)		0,2	0,5	1,0		
Stock estimate (tonnes)		10×10^6	8×10^6	12×10^6		

As pointed out above, the hydrography of the southern Benguela region offshore of the continental shelf break suggests that in the main there should be a mixed temperate–subtropical mesopelagic fauna. The results indicate that this is true and that temperate species (52%) and subtropical species (19%) comprise about 71 per cent of the total lanternfish fauna. The compositional value for the broadly tropical element—i.e. those species distributed in both tropical and subtropical waters—approximates that of the subtropical element, while widespread species comprise about 10 per cent of the myctophid fauna.

All Atlantic widespread species are found in the southern Benguela region, namely *Diogenichthys atlanticus, Electrona risso, Lobianchia dofleini* and *Notolychnus valdiviae*. The Warm Water Group, which comprises about 37 per cent of the fauna, includes Holoeurytropical, Thermophobic-eurytropical, Bisubtropical and South subtropical Subpattern species. The percentage contribution of each of these subpatterns to the myctophid fauna ranges between 7 and 11 per cent (Fig. 2). Of the 12 holoeurytropical species known from the Atlantic Ocean, six species *(Centrobranchus nigroocellatus, Diaphus subtilis, Gonichthys cocco, Hygophum reinhardtii, Loweina rara, Notoscopelus caudispinosus)* have not been recorded in the southern Benguela region. *Lampadena chavesi* and

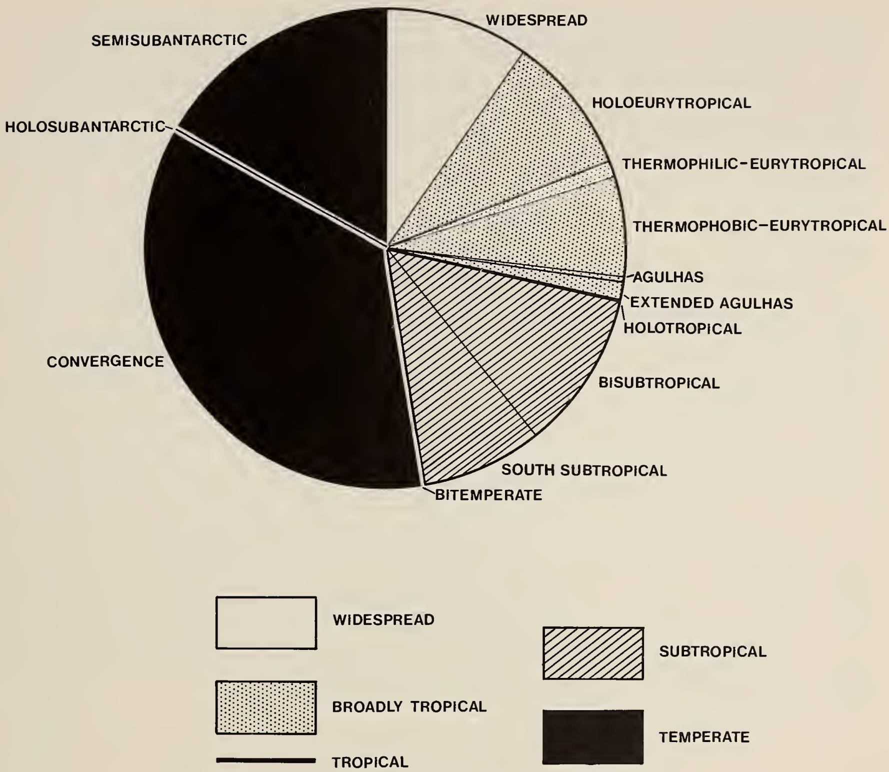

Fig. 2. Percentage composition by pattern and subpattern of high-oceanic species of Myctophidae, based on catch rates of RMT–2, RMT–8 and MT–1600 nets from SFRI Phyllosoma Surveys and from *Walther Herwig* stations in the southern Benguela region.

Taaningichthys minimus (Bisubtropical Subpattern: 9 Atlantic species) and *Diaphus anderseni* (South subtropical Subpattern: 4 Atlantic species) have also not been recorded. All Thermophobic-eurytropical Subpattern species known from the Atlantic have been taken in the region. The somewhat low percentage contribution of species of this subpattern is difficult to interpret at this stage; it may be due either to a sampling artifact or related to the small number of species involved *(Lampanyctus lineatus* is an uncommon species with a night distribution at 150–350 m and 900–1 000 m—Nafpaktitis *et al.* 1977), or both.

Cool Water Group temperate species, which comprise about 52 per cent of the myctophid fauna in the southern Benguela region, include bitemperate (<1%), convergence (35%), semisubantarctic (17%), and holosubantarctic (<1%) species (Table 8). This confirms the strong intrusion of southern elements into the southern Benguela region, particularly those species associated with the Subtropical Convergence and with the region between the Convergence and the Subantarctic Divergence, and agrees with the conceptual image of the region derived from physical studies. Whether this compositional structure changes with decreasing latitude is difficult to assess, since comparative data are not given by Rubiés (1985) for the South West African–Namibian myctophids. However, he has pointed out (p. 581) that most are subtropical species and that 'subantarctic' species, i.e. 'coming from the Convergence area', were caught in very small numbers.

Stock estimate

Mean catch rates for each subpattern (specimens/1 000 m^3) for the PAUG82 (RMT–2), PAUG83 and PAUG84 (RMT–8) and WH–71 (MT–1600) cruises have been calculated from abundance values (specimens/hour). These are presented in Table 8. Estimates of the stock of lanternfishes in the offshore area of the eastern South Atlantic are calculated as 10×10^6 tonnes in the case of sampling with an RMT–2; 8×10^6 tonnes with an RMT–8; and 12×10^6 tonnes with an MT–1600 net. The mean value (10×10^6 tonnes) represents about 62 per cent of the abundance estimate for mesopelagic fishes of the South-east Atlantic (Gjøsaeter & Kawaguchi 1980) and compares with the lanternfish composition by number (56%) for Transect II of the 1971 cruise of FRV *Walther Herwig* (Hulley 1981). However, this transect also encompassed subtropical and tropical regions. Since Hulley & Krefft (1985) have demonstrated that smaller populations of myctophids occur in warm-water species than in cold-water species, the mean stock estimate of 10×10^6 tonnes appears to be realistic.

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